

SPATIAL AND TEMPORAL PATTERNS IN A SAGEBRUSH STEPPE SPIDER COMMUNITY (ARACHNIDA, ARANEAE)

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ABSTRACT

A total of 83 species of spiders were collected from the shrub, herb and ground strata of a sagebrush steppe in northern Utah. Dominant families (Thomisidae, Philodromidae, Salticidae) and, in some cases, genera (*Misumenops*, *Philodromus*) or species [*Sassacus papenhoei* (Peckham and Peckham)] were similar to those found in other studies of shrub-dominated areas. Among the spiders of this community, ambushing and wandering were more common foraging strategies than was webspinning.

Habitat separation in sagebrush steppe spiders was more vertical than horizontal. Shrub and herb spider species assemblage differed sharply from the ground spider species assemblage, less so from one another. Differences in vegetation density, diversity and size among four study plots correlated positively with spider abundance and diversity, but resulted in less difference among spider assemblages.

Temporal patterns of spider abundance differed among strata. Seasonal patterns showed evidence of being influenced by climate and migration of spiders between strata. Diel activity patterns were examined only for spiders of shrub and herb strata. Spider activity in the herb stratum was strongly influenced by light intensity, temperature and relative humidity. This was not as clear in shrubs.

INTRODUCTION

In order to understand the structure and processes of spider communities in shrub-dominated areas, one must obtain knowledge of the distributions of spiders in shrub, herb and ground strata. With the exception of Gertsch and Riechert (1976), few studies have accomplished this. Most studies have examined the spiders of one community stratum. For example, Chew (1961) and Chaplin (1976) studied the spiders of hot and cold desert shrubs, respectively. Fautin (1946) included data on shrub stratum spiders in his study of western Utah biotic communities, and Hatley and MacMahon (1980) outlined seasonal distributions of spiders in sagebrush. Turner (1962) included ground stratum spiders in his sampling study of plants and arthropods in Arizona desert.

Other spider studies in shrub-dominated areas have concentrated on single species (e.g., Riechert 1974) or families (e.g., Bixler 1970). Habitat partitioning among some common sagebrush steppe spiders was examined by Robinson (1981).

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The purposes of the present study are: (1) To describe the taxonomic composition of the spider community of a sagebrush steppe in northern Utah; (2) To describe and compare distributions of spider species, families and foraging strategies (ambushing, wandering, webspinning) (a) among shrub, herb and ground strata, (b) among study plots having a continuum of vegetation types (herbaceous—herbaceous/shrubby—shrubby), (c) seasonally and (d) through the day; (3) To examine correlations of spider distributions with climatic variables and characteristics of the vegetation (density, diversity, cover, height, volume).

STUDY AREA

The study was conducted on the upper alluvial fan at the mouth of Green Canyon, Cache Co., Utah (elevation 1512 m). Mean annual temperature for the area is 7.9°C; mean annual precipitation is 46.8 cm (mostly snow); mean number of frost-free days is 145 (A. Richardson, Utah State Climatologist, personal communication).

Vegetation is sagebrush steppe, dominated by *Artemisia tridentata* (Pursh) Scribn. and Smith. Other shrubs in the area are *Amelanchier alnifolia* Nutt., *Chrysothamnus nauseosus* (Pall.) Britton, *Gutierrezia sarothrae* (Pursh) Britton and Rusby, and *Rosa woodsii* Lindl. Grasses are *Agropyron spicatum* (Pursh) Scribn. and Smith, *Bromus brizaeformis* Fischer and Meyer, *B. commutatus* Schrader, *B. tectorum* L., *Poa bulbosa* L., *P. pratensis* L., *Secale cereal* L., and *Stipa* sp. Some abundant herbaceous species are *Alyssum alyssoides* L., *Erodium cicutarium* L'Her., and *Ranunculus testiculatus* Crantz., which are very small and carpet the ground in some areas. Other common herbs on the study site are *Achillea millefolium* L., *Artemisia ludoviciana* Nutt., *Astragalus cibarius* Sheld., *Balsamorhiza sagittata* (Pursh) Nutt., *Camelina microcarpa* Andr., *Crepis occidentalis* Nutt., *Cymopterus longipes* S. Wats., *Hackelia patens* (Nutt.), *Lithospermum ruderae* Dougl., *Phacelia linearis* (Pursh), *Solidago canadensis* L., *Sonchus oleraceus* L., *Tragopogon dubius* Scop., and *Wyethia amplexicaulus* Nutt.

Soil at the canyon's mouth (on which were Study Plots, 2, 3 and 4) was Loamy-skeletal, mixed, mesic Typic Calcixeroll. On the slope above the alluvial fan (containing Plot 1) soil was Loamy-skeletal, carbonatic, mesic Typic Haploxeroll (Erickson and Mortensen 1974). Stones were numerous on the surface of Plot 1.

METHODS

Study Plots.—Four 3600 m² study plots were established and subdivided into 12 x 12 m squares. Vegetation was sampled on the plots in June and July 1974. Density, height, cover and volume (formulae as in Hatley and MacMahon 1980) of shrubs were determined in 10 randomly located 2 m x 8 m quadrats within each plot. Density, cover class (Daubenmire 1959) and height class (0-25 cm, 26-50 cm, 51-75 cm, over 75 cm) were determined for each herb species in seven 20 cm x 50 cm microplots within each 2 m x 8 m quadrat.

Spider Sampling.—Spiders were sampled from August through September 1974, June through October 1975 and May through November 1976. Three of the four study plots burned in a range fire in July 1976; subsequent sampling was completed in the remaining plot (#1). As a consequence, number of samples in the plots differed.

Spiders in herbaceous vegetation were sampled with a sweep net, by taking 100 sweeps while walking 100 paces parallel to plot grid stakes. Four 100-sweep samples were taken at each sampling time. Subsequent samples in the same area were taken at intervals of at least two weeks. The total number of 100-sweep samples was 458.

Shrub-inhabiting spiders were dislodged by beating shrubs with a stick, knocking the spiders onto sheets. Three shrubs were sampled at each sampling time. Except in Plot 1, no shrub was sampled more than once. A total of 354 shrubs were sampled.

Ground-dwelling spiders were sampled with pitfall traps similar to those of Uetz and Unzicker (1976), but without a rim. A sampling station consisted of three pitfall traps located within 30 cm of each plot grid stake. Each plot had 108-111 pitfalls. Pitfall samples in the same area were taken at intervals of at least two weeks. Samples varied in number of trap-hours; total trap-hours were 22,329.

Discussion of these sampling methods may be found in Uetz and Unzicker (1976) and Southwood (1978). Turnbull (1973) concluded that the sampling method of choice depends upon the community to be sampled. I chose the above methods because: (1) No absolute densities were to be calculated; (2) Samples were to be taken by one person, frequently at night; and (3) These methods are inexpensive, easy to use, and relatively immune to equipment failure. Realizing that no completely error-free method for quantitative sampling of small, active arthropods exists, I am satisfied that my methods adequately surveyed the spider fauna. Graphs of cumulative sample variance of spider families against randomized accumulated samples in each stratum indicated adequate sampling after 50 samples (Figure 1). Similar curves for species did not quite level off after 300 samples for shrub and ground strata, perhaps due to rare immigrants from adjacent communities.

All spiders were picked from samples in the field and preserved for laboratory identification. Species, sex (if determinable) and body length excluding spinnerets were recorded for each specimen. Species were kindly identified by Dr. W. J. Gertsch.

Local Environment—Time of day, temperature, relative humidity and light intensity were recorded before and after each sampling period. During 1975 and 1976 a hygrothermograph and an actinograph also recorded continuous data on the study site. Monthly precipitation data were obtained from a weather station in North Logan (one km from the study site) (Figure 2).

Spider Data Analysis.—Data on shrub-, herb- and ground-dwelling spiders were analyzed separately because of the different sampling techniques used in each stratum. For seasonal patterns, the data were grouped into 15 biweekly intervals beginning 5 May (first sample) and ending 29 November (last sample). For daily patterns, data were numbered

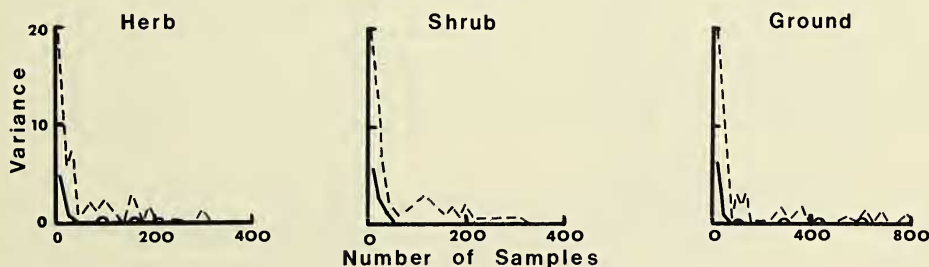


Fig. 1.—Variance in number of spider families (solid lines) and species (broken lines) in randomized, accumulated samples from community strata at Green Canyon, Cache Co., Utah.

by midpoint of sampling time (e.g., 0730–0829 = 0800 hr). Data on ground-inhabiting spiders could not be analyzed hourly, because sampling duration was greater than one hour. (Few ground spiders were captured in one hour.)

Spider diversities were calculated using the Shannon-Wiener Diversity Index (Shannon and Weaver 1949). Horn's (1966) Index of Overlap was chosen to examine similarity of spider assemblages in space and time. Any two spider assemblages scoring over 85% on Horn's Index were considered arbitrarily "similar". Huhta (1979) listed Horn's Index as one of six indices which gave consistent results; Linton, Davies and Wrona (1981) found that Horn's Index was as accurate as other overlap indices between 75 and 100% overlap.

For some analyses, spider families were grouped into three foraging strategies (ambushing, wandering, webspinning; see Appendix). These categories were largely based on accounts in the literature (e.g., Gertsch 1979) and personal observation of spider hunting. This method assumes a constant foraging strategy within spider families. Spider families are constructed on the basis of morphology, which is often correlated with the method of prey capture. Post and Riechert (1977) thought that adaptive syndromes such as hunting techniques emerge at the family level rather than at the species level in spiders.

An initial five-way analysis of variance (ANOVA) was used to determine whether interactions between variables were significant. The five variables were stratum, plot, year, biweekly interval and time of day. Interactions were not significant, and years were not significantly different. Spider data for the three study years were therefore lumped, and compared in spatial (plots) and temporal (biweekly, hourly) categories within strata by one-way ANOVA. Student-Newman-Keuls Multiple Range Tests (SNKMRT) for unequal sample sizes were performed on means when ANOVA was significant. (In this paper, statistical significance is $P = 0.05$ or less unless otherwise noted.) Since SNKMRT is not as powerful a test as ANOVA, it did not always detect which means were different.

Abundance of individuals and dominant spider families was regressed against characteristics of the vegetation. Since sampling the vegetation of the four study plots gave only four data points, two-variable linear regressions were employed to compare one vegetation parameter at a time with spider abundance.

Spider abundances were used in stepwise multiple regressions against the following components of local environment: temperature, relative humidity, light intensity, vapor

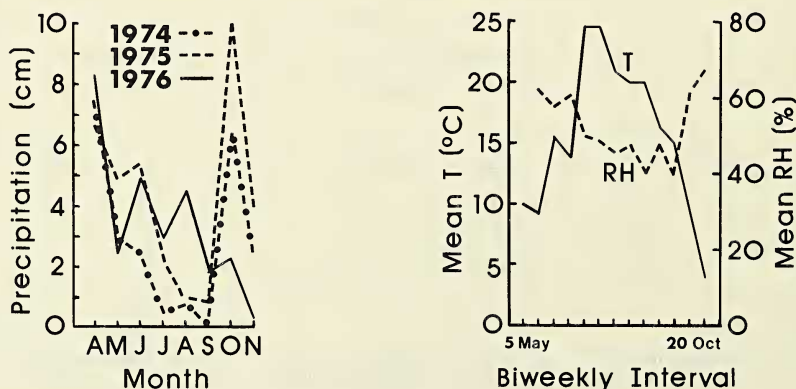


Fig. 2.—Seasonal weather patterns at Green Canyon, Cache Co., Utah. Monthly precipitation curves are from the North Logan weather station; temperature and relative humidity curves are from a hygrothermograph on the study site (1975 only).

pressure deficit and hours of daylight on the sampling date. Biweekly averages of temperature, relative humidity, minimum temperature and daily high light intensity during 1975 were used to test for longer-term relationships.

RESULTS AND DISCUSSION

Taxonomic Composition and Vertical Stratification of the Spider Community.—

In the present study, 11,098 spiders representing 83 species and 18 families (see Appendix) were collected from a combined area of slightly over one ha (10,800 m²). Table 1 summarizes spider sampling data from shrub, herb and ground strata. When all vertical strata of a community are examined, more spider species appear than are present in one stratum alone. Hatley and MacMahon (1980), working only in the shrub stratum at Green Canyon, found 40 species of spiders, as compared to 83 species found in all community strata by the present study. Turner (1962) found that ground stratum spiders of the Arizona desert were completely different (with the exception of one *Oxyopes* specimen) from those swept from Arizona desert shrubs by Chew (1961).

Table 2 summarizes the numerically dominant spider families and species in each community stratum. Thomisidae was by far the dominant in herbs, while Lycosidae, Gnaphosidae and Thomisidae were numerically dominant on the ground. In shrubs, dominant families were Salticidae, Theridiidae, Philodromidae and Thomisidae. Only two spider species in herbs [*Misumenops lepidus* (Thorell) and *Xysticus cunctator* Thorell], three in shrubs [*Theridion neomexicanum* Banks, *Sassacus papenhoei* (Peckham and Peckham) and *Philodromus histrio* (Latreille)] and three on the ground (*Schizocosa wasatchensis* Chamberlin and Ivie, *Xysticus montanensis* Keyserling and *Drassyllus nannellus* Chamberlin and Gertsch) attained 10% of the spider fauna of their respective stratum.

Comparing these results to those of other studies in shrub-dominated areas shows some similarities. Fautin (1946) recorded spiders of Utah cold desert shrubs; Chew (1961) studied spiders in Arizona creosotebush (*Larrea*); Chaplin (1976) worked with spiders of Nevada greasewood (*Sarcobatus*) and shadscale (*Atriplex*). *S. papenhoei*, a jumping spider, was a dominant in shrubs of Chew's, Chaplin's and the present study, and in one of Fautin's areas. *Philodromus*, a philodromid crab spider, was important in all four studies, and *Misumenops*, a crab spider, was dominant in Chew's, Fautin's and the present study.

Comparison of these four studies also revealed differences. In all studies but Chew's, one dominant species was a web spider. In Chaplin's study, *Dictyna*, a cribellate cobweb weaver, was numerically dominant during mid- and late summer. *Metepeira foxi* Gertsch and Ivie, an orb weaver, was common in Fautin's study. Both of these species were common in the present study, but *T. neomexicanum*, a combfooted cobweb weaver, was the most abundant spider in shrubs. Chew attributed a relative lack of web spiders in hot desert shrubs to flexible shrubs, wind, and less well-developed vegetational stratification in hot deserts.

The Green Canyon study site had strong morning and evening "canyon winds", but sagebrush steppe has a better-developed herbaceous stratum than hot desert, and cold desert shrubs such as greasewood, shadscale and sagebrush supply less flexible, less open substrate than does creosotebush. Robinson (1981) reported that *T. neomexicanum* and *M. lepidus* were the most abundant spiders collected from experimental habitat modules placed near the Green Canyon plots used in the present study. He found that *M. lepidus*

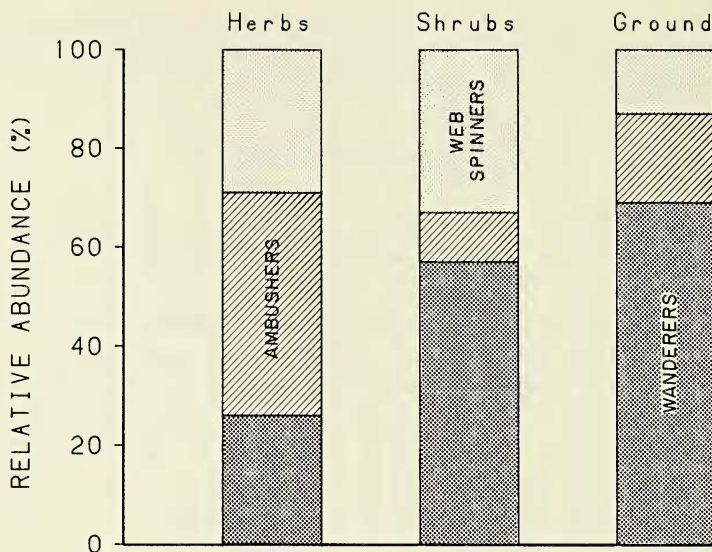


Fig. 3.—Relative abundance of three spider foraging strategies among individuals in herb, shrub and ground strata of the sagebrush steppe at Green Canyon, Cache Co., Utah.

showed no preference for open or closed, horizontal or vertical substrate, whereas *T. neomexicanum* preferred closed habitat. Hatley and MacMahon (1980), also working at Green Canyon, found that web spiders (mostly *Theridion* spp.) on sagebrush preferred dense to open foliage. They found no preference for dense or open foliage in running spiders (mostly *P. histrio*). These results combine to clarify the dominance of crab spiders (*Misumenops* and *Philodromus*) in both the hot desert and cold desert shrubs which have been studied: they are habitat generalists. Conversely, web spiders such as *Theridion* and *Dictyna* are probably limited in their distributions by shrub architecture.

At the species level, web spiders can be important members of shrub-dominated communities. However, capturing prey in webs is less common than other foraging strategies used by spiders in these areas. One spider foraging strategy reached its peak abundance in each stratum of the sagebrush steppe (ambushers in herbs, wanderers on the ground and webspinners in shrubs) (Figure 3). In herbs and on the ground, these respective strategies were dominant, but even in shrubs wanderers were more abundant than webspinners. Chew (1961) found that 94% of individuals and 79% of species in shrubs were non-webspinners (crab spiders and jumping spiders). Chaplin (1976) found shrub spider biomass to be dominated by crab spiders and jumping spiders. Fautin (1946) found 70% of shrub spider species to be non-webspinners. In the sagebrush of the present study, non-webspinning spiders comprised 67% of individuals and 55% of species sampled. Herb and ground stratum spiders were dominated by non-webspinners to an even greater degree.

Chew's (1961) finding that the spider community of hot desert shrubs is dominated by non-webspinning spiders can be generalized to include all strata of shrub-dominated areas. In spite of differences in rainfall, shrub architecture and vertical stratification among hot and cold deserts and sagebrush steppe, there remains a "shrubs community spider fauna" characterized by dominance of non-webspinning spiders.

Post and Riechert (1976) found that dominant spiders were often habitat generalists. Most spider taxa collected from vegetation in the present study were found in both herb

Table 1.—Characteristics of the spider community in vertical strata of the sagebrush steppe at Green Canyon, Cache Co., Utah.

Characteristic	Herbs	Stratum Shrubs	Ground
No. of spiders collected	6633	2874	1591
No. of spider families	14	13	16
No. of spider species	61	55	50
diversity (H')	2.652	2.659	2.632
evenness (J')	0.645	0.664	0.673

and shrub strata. The top dominant species in herbs and shrubs (Table 2) were each over 5% of the spider fauna in the other vegetative stratum. (Each stratum had only 3-6 species which were over 5% of the spider fauna. See Appendix.) Pairwise comparisons of Green Canyon spider assemblages in strata showed much more similarity between the vegetational strata than between either vegetational stratum and the ground (Table 3). The herb stratum seemed to function as an ecotone, separating typical ground and shrub spider communities, with additional species begin most common in this "edge" habitat. This resulted in both the highest species richness and the highest dominance being observed in herb stratum spiders (Table 1).

Turnbull (1960) found that the field layer (herb stratum) in English oak woods contained spiders from both ground and canopy strata. Luczak (1966, in Turnbull 1973) attributed the greatest number of spider species and individuals to the field layer. She suggested that this might cause competition, forcing spiders to migrate upward. Lowrie (1968) documented movement of mature wandering spiders out of the herb stratum, into both ground and canopy layers.

In the present study the ground spider fauna was most restricted; no ground dominant was taken regularly in vegetation. [Robinson (1981) identified a dominant on his artificial habitat modules at Green Canyon as *X. montanensis*, a species which was restricted to

Table 2.—Numerically dominant spider species and families from vertical strata of the sagebrush steppe at Green Canyon, Cache Co., Utah. Prominence of Thomisidae in shrubs is due to cumulative abundance of several species each comprising less than 10% of shrub spiders. For number captured and relative abundance of each species, see Appendix.

DOMINANTS				
Stratum	Family Rank	Family	Species	Species Rank
Herbs	1	Thomisidae	<i>Misumenops lepidus</i>	1
		Thomisidae	<i>Xysticus cunctator</i>	2
Shrubs	1	Salticidae	<i>Sassacus papenhoei</i>	2
	2	Theridiidae	<i>Theridion neomexicanum</i>	1
	3	Philodromidae	<i>Philodromus histrio</i>	3
	4	Thomisidae	—	—
Ground	1	Lycosidae	<i>Schizocosa wasatchensis</i>	1
	2	Gnaphosidae	<i>Drassyllus nannellus</i>	3
	3	Thomisidae	<i>Xysticus montanensis</i>	2

Table 3.—Horn's (1966) Index of Overlap pairwise comparisons of species level spider assemblages in vertical strata and four study plots within the sagebrush steppe at Green Canyon, Cache Co., Utah. 100% overlap is identity; 85% or greater is considered "similar".

Strata	% Overlap		
Herbs: Shrubs	73.1		
Herbs: Ground	17.7		
Shrubs: Ground	17.4		
Strata within Plots:			
Plots	% Overlap in Herbs	% Overlap in Shrubs	% Overlap on Ground
1: 2	90.4	91.9	82.3
1: 3	90.2	89.1	85.9
1: 4	84.3	88.0	79.2
2: 3	95.9	93.6	94.5
2: 4	90.8	93.6	84.0
3: 4	90.6	90.7	85.6

the ground in the present study. Hatley (1978) did not find this species above the ground at Green Canyon. I feel certain that Robinson's *Xysticus* was actually *X. cunctator*, which both Hatley and I collected in abundance on foliage; the latter identification was verified by W. J. Gertsch.] Previous authors have also found ground spider faunas to be distinct from those of vegetation (Turnbull 1973, Chaplin 1976, Culin and Rust 1980). This is thought to reflect a discontinuity between microclimates of the ground and vegetation (Elliott 1930, Gibson 1949, Turnbull 1960). Riechert and Tracy (1975) demonstrated that temperature can restrict ground spider activity, while Gertsch and Riechert (1976) considered that temperature stress is probably negligible for spiders inhabiting shrubs and tops of grass clumps.

In summary, the most important factor causing vertical stratification of spiders in the sagebrush steppe seems to be differential availability of appropriate substrate for foraging or web-building. However, effects of vegetation on spider distributions cannot entirely be separated from those of microclimate (Turnbull 1973), because plant cover greatly modifies microclimate (Geiger 1965).

Effects of Vegetation on Spiders of the Four Study Plots.—Similar plant communities have characteristic spider faunas (Barnes and Barnes 1955, Berry 1970); different plant communities have different associations of spiders (Muma 1973, Gertsch and Riechert 1976). Within a coniferous forest in northeastern Minnesota, Stratton, Uetz and Dillery (1979) found significant differences in spider families present on three tree species. One would therefore expect differences in vegetation within the sagebrush steppe to be paralleled by changes in the spider fauna. Differences in vegetation among the four study plots of the present study are described in Table 4.

Differences in spider assemblages (Table 5) were observed where vegetation differed among the four study plots. ANOVA on number of spiders in the plots was significant at $P = 0.01$ or less for each stratum. Numbers of spiders in dominant families of each stratum were significantly different among plots except for Lycosidae and Theridiidae. However, pairwise comparisons of plots for spider assemblages of strata showed overlap to be generally high (Table 3). Differences in distributions of spider foraging strategies

among the study plots were not as great as differences among strata (Figure 4). Habitat separation in sagebrush spiders seems to be more vertical than horizontal at this gross level of analysis.

HERB STRATUM. Three measures of herb stratum habitat diversity correlated with spider species richness: herb height class diversity ($r = 0.95$), herb height class evenness ($r = 0.98$), and herb species diversity ($r = 0.98$). The importance of physical structure and heterogeneity of the environment to spider distributions has been amply documented (Curtis and Morton 1974, Colebourn 1974, Gertsch and Riechert 1976, Muhlenberg et al. 1977, Lubin 1978, Uetz 1979, Hatley and MacMahon 1980, Robinson 1981).

In the present study Plot 1 provided the most diverse and abundant substrate for spiders in the herb stratum (Table 4). This was correlated with the highest spider species richness, diversity and evenness of any plot (Table 5). High diversity of herb species and cover classes, coupled with low cover class evenness, resulted in some large unispecies patches of herbs. Sampling these patches probably reduced the mean number of spider species per sample in Plot 1. Plot 2 generally had intermediate vegetational characteristics and an intermediately abundant foliage spider fauna (Table 5).

Although having generally intermediate substrate diversity, Plot 3 had the highest number of spiders and species per sample. This may have been the result of low grass density. Number of spiders in the herb stratum of each plot was negatively correlated to grass density in that plot ($r = 0.98$). Muma and Muma (1949) found grass to be a poor substrate for web spiders, and Lowrie (1968) suggested that flexible, non-woody vegetation provided unsuitable substrate for large wandering spiders. In the present study, webspinners of the herb stratum were significantly least abundant in Plot 1 (which has

Table 4.—Characteristics of the plant community in four study plots at Green Canyon, Cache Co., Utah.

Vegetation Characteristic	PLOT			
	1	2	3	4
<i>Artemisia tridentata</i>				
density (#/m ²)	0.09	0.12	0.18	0.93
\bar{x} height (cm)	73.2	68.2	63.8	37.3
\bar{x} cover	3552	8780	3103	670
# height classes	5	6	7	4
height class diversity	1.415	1.574	1.687	1.184
<i>Herbaceous vegetation</i>				
species diversity (H [†])	2.002	1.532	1.527	1.266
evenness (J [†])	0.589	0.496	0.458	0.457
# species (s)	30	22	28	16
density (#/m ²)	1022	1313	1248	2022
density of ground carpet ¹	557	865	893	1626
density of grass	428	421	290	388
% herbs over 25 cm tall	27.4	16.7	10.8	1.7
cover class diversity	1.142	1.197	0.913	1.036
cover class evenness	0.637	0.668	0.567	0.644
height class diversity	0.873	0.590	0.397	0.089
height class evenness	0.630	0.426	0.361	0.081

¹*Erodium cicutarium* and *Alyssum alyssoides*. See "Study Area".

Table 5.—Characteristics of the spider community in four study plots at Green Canyon, Cache Co., Utah.

Stratum	PLOT			
	1	2	3	4
HERBS				
# 100-sweep samples	131	116	105	106
# spiders collected	1503	1557	2083	1490
\bar{x} spiders/sample	11.5	13.4	19.8	14.1
\bar{x} species/sample	5.2	5.4	6.7	5.1
diversity (H')	2.661	2.497	2.522	2.501
evenness (J')	0.684	0.648	0.659	0.678
# species (s)	49	47	46	40
SHRUBS				
# shrubs sampled	93	89	86	86
# spiders collected	926	824	819	305
\bar{x} spiders/shrub	10.0	9.3	9.5	3.5
\bar{x} species/shrub	3.8	3.8	4.1	2.1
diversity (H')	2.585	2.519	2.625	2.530
evenness (J')	0.675	0.709	0.712	0.730
# species (s)	46	35	40	32
GROUND				
# trap-hours	13,619	3517	3193	2000
# spiders collected	659	325	376	231
\bar{x} spiders/100 trap-hours	7.8	12.8	13.2	15.4
\bar{x} species/100 trap-hours	1.5	0.9	1.0	1.3
diversity (H')	2.327	1.948	2.038	2.190
evenness (J')	0.615	0.630	0.619	0.689
# species (s)	44	22	27	24

the highest grass density); wanderers and ambushers of the herb stratum were significantly most abundant in Plot 3 (which had the lowest grass density).

In addition to its flexibility, grass presents an essentially vertical substrate, which may be unsuitable for small web-spinning spiders which prefer complex substrate (Hatley and MacMahon 1980, Robinson 1981). In the present study Dictynidae and Araneidae were least abundant where grass was most dense.

Plot 4 provided the sparsest, shortest and least diverse herb stratum and had the lowest spider species richness and low spider species diversity, but an intermediate number of spiders per sample in herbs. The latter may have been due to the low density of grass.

SHRUB STRATUM. Number of spiders per shrub was correlated to size of shrub, but coefficients of determination (r^2) were low (height = 0.31, cover = 0.40, volume = 0.31, all three = 0.43). The large shrub size in Plot 1 probably contributed to the highest number of spiders and species per shrub being in that plot. Chaplin (1976) found a correlation between shrub volume and spider numbers. Hatley (1978) suggested that larger shrubs are more diverse habitats and so should contain more species of spiders. Robinson (1981) found that numbers of spiders increased with increasing amount of substrate in artificial habitats. Another reason for the correlation of shrub height to spider abundance might be that taller shrubs catch more immature, ballooning spiders. (Spiders collected in shrubs in the present study were 95% immature.)

The sparseness (habitat island effect) of shrubs in Plot 1 and the lack of height diversity did not seem to reduce spider species richness or diversity (Table 5). However, most shrub spiders were also found in the herb stratum (see Appendix), so that shrubs were surrounded by potential faunal source areas. The abundant herb stratum of Plot 3 may also have contributed to the highest number of species per shrub and species diversity being in that plot, but Plot 3 also had a much denser shrub stratum and the highest diversity of shrub heights (Table 4).

In spite of high shrub density in Plot 4, small shrub size and lack of shrub size diversity probably led to this plot having the lowest spider species richness, diversity and number of spiders per shrub. There were significantly fewer Salticidae and Philodromidae in shrubs of Plot 4. Hatley and MacMahon (1980) found correlation between shrub height and numbers of Philodromidae and between shrub height, cover and volume and numbers of Salticidae at Green Canyon.

GROUND STRATUM. Ground-dwelling spiders were most abundant in Plots 3 and 4, which had high densities of very short vegetation (Table 4). This ground carpet may have moderated microclimate, thus establishing a more optimal environment for ground spiders. Dryness may have limited ground spiders in Plot 1, which had significantly fewest spiders per sample. Soil permeability of each plot was the same, but the water capacity of Plot 1 was slightly lower (Erickson and Mortensen 1974). In addition, cold air drainage from the canyon should have maintained a slightly higher relative humidity on the other plots. Plot 1 was slightly removed from this drainage, on a west-facing slope, and so may have had a drier microclimate. Several important groups of ground spiders had significant correlations with relative humidity.

Rocks on the surface of Plot 1 increased habitat heterogeneity by providing retreats for ground spiders. This may explain why Plot 1 had the highest species richness, diversity and number of species per sample (Table 5). One would expect to find more ground-dwelling spiders where that stratum is structurally diverse (Williams 1959, Uetz 1979).

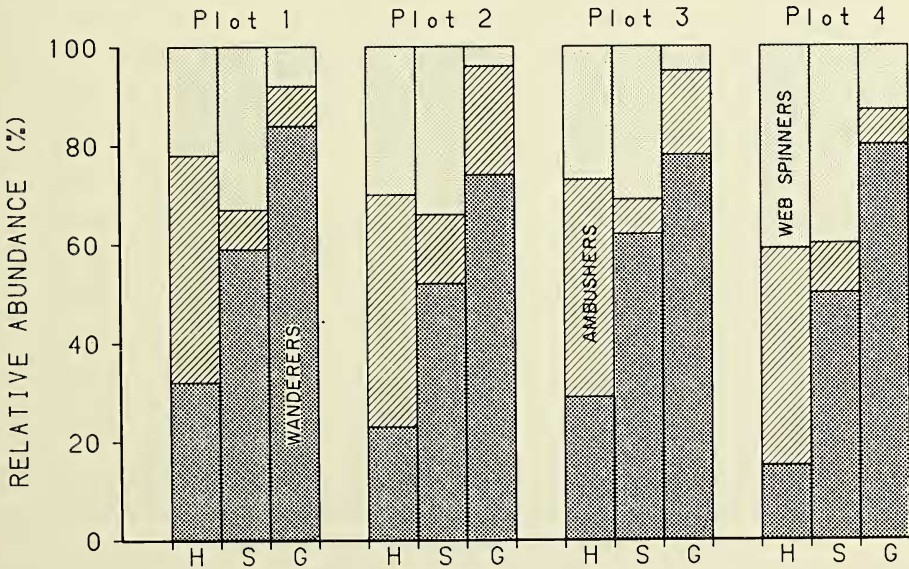


Fig. 4.—Relative abundance of three spider foraging strategies among individuals in herb, shrub and ground strata in four study plots at Green Canyon, Cache Co., Utah.

Plot 2, which was most similar to Plot 1, had few rocks on the soil surface, an intermediate number of spiders per sample, and the lowest spider species richness, diversity and number of species per sample.

Conclusions: Spatial Patterns.—The preceding discussion of spatial patterns in spider communities of the sagebrush steppe has stressed the role of substrate for spider foraging, and microclimate, which is not independent of vegetation. These seem to be the most important proximate characteristics of the environment determining spider distributions.

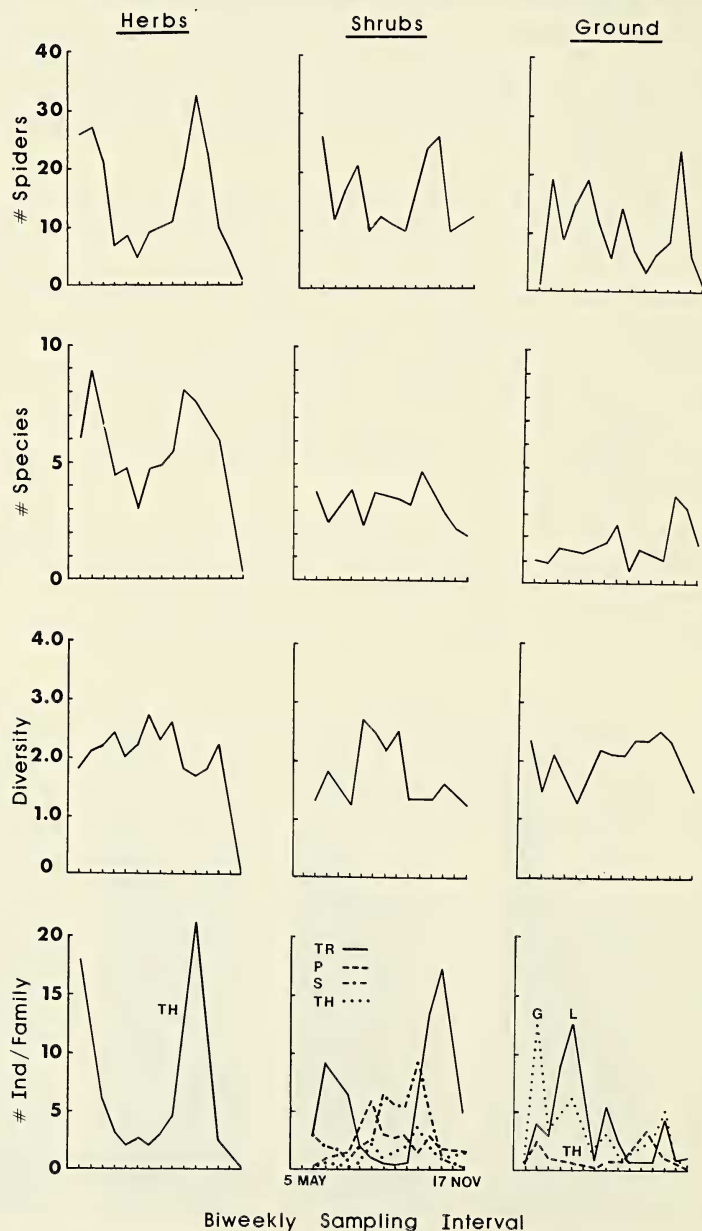


Fig. 5.—Seasonal abundance and diversity of spiders in herb, shrub and ground strata of the sagebrush steppe at Green Canyon, Cache, Co., Utah. All values are means/sample. TH = Thomisidae; TR = Theridiidae; P = Philodromidae; S = Salticidae; L = Lycosidae; G = Gnaphosidae.

Riechert and Tracy (1975) constructed a model which suggested more optimal energetics for spiders which chose the correct thermal environment rather than the environment having the most prey. Different spider foraging strategies predominate in different strata of the sagebrush steppe, due to suitability of substrate structure and microclimate. Greenquist and Rovner (1976) found differences in lycosid hunting techniques in different strata of artificial environments. Stratton, Uetz and Dillery (1979) attributed the dominance of space web spiders and orb web spiders on different coniferous tree species to substrate structure.

Nevertheless, Uetz (1977) found that weather and habitat structure were not enough to explain spider distributions. Other important elements of habitat, such as prey availability, were not evaluated in the present study. Spiders are generally considered to be polyphagous predators (Turner and Polis 1979, Olive 1980, Nyffeler and Benz 1981). Habitat characteristics favoring large numbers of spiders should also favor large numbers of suitable prey (other small arthropods). For example, Uetz (1979) found significant increases in prey species richness with increases in litter depth.

Temporal Patterns.—SEASON. In the herb stratum, spider abundance and species richness showed a spring peak followed by a summer decline, an autumn peak and a final decline to nearly zero by the end of November (Figure 5). The same abundance pattern was shown over the three years of the study and in all four study plots (Figure 6). This pattern was significant for the dominant spider family in the community (Figure 5).

MacMahon and Trigg (1972), working in the herb stratum of an Ohio old field, also found early and late season peaks in spider abundance. They attributed this pattern to phenology, rather than seasonal change in species composition of the spider community such as that which Evans and Murdoch (1968) found in adult insects of a Michigan old field.

Abundance patterns of spiders through the season may be explained as follows. Addition of individuals and species in spring was due to gradual emergence of overwintering spiders. Peak spring abundance was partly due to reproduction by spiders which had overwintered as adults or penultimate instars. The decline in number of spider species, as well as individuals, captured during midsummer suggest that phenology alone does not account for the observed pattern (Figure 5). The summer decrease in herb spider and species abundances may have been due to (1) mortality during the hot, dry part of the year (figure 2), (2) dormancy to avoid heat or water stress, or (3) dispersal out of the herb stratum or the area.

Although during June decreasing herb spider abundance coincides with increasing ground spider abundance, the latter is explained by large numbers of immature Lycosidae being captured on the ground at this time (Figure 5). The present study provides no evidence for aestivation on the ground by herb stratum spiders during the hot part of the summer.

The June decrease in herb stratum spiders also coincide with an increase in shrub stratum spiders which was not due to reproduction of the latter (Figure 5). This may indicate movement of spiders out of herbs into shrubs during the hottest part of the summer (Figure 2). Within shrubs temperature extremes are moderated. While shrub stratum spider abundance increased late in June, diversity decreased. This may have been caused by many Thomisidae moving into shrubs at this time (Figure 5).

Dispersal of juvenile spiders after spring reproduction would certainly decrease numbers of herbs stratum spiders, but probably as many spiders dispersed into the study area as out of it. The present study cannot determine whether net emigration accounted for the low summer abundance of spiders in the herb stratum.

Spring and summer peaks in ground spider abundance were each due to a significant peak in a dominant ground spider family—Gnaphosidae in May and Lycosidae in June (Figure 5). Autumn peaks in foliage spider abundance were due to reproduction by Thomisidae in herbs and Theridiidae in shrubs (Figure 5).

The winter decline in foliage spider abundance was undoubtedly due to spider migration out of vegetation to overwintering sites on the ground (Elliott 1930, Moulder and Reichle 1972). Ground spider abundance peaked simultaneously due to this influx from other strata. At the same time number of spider species was also decreasing in vegetation

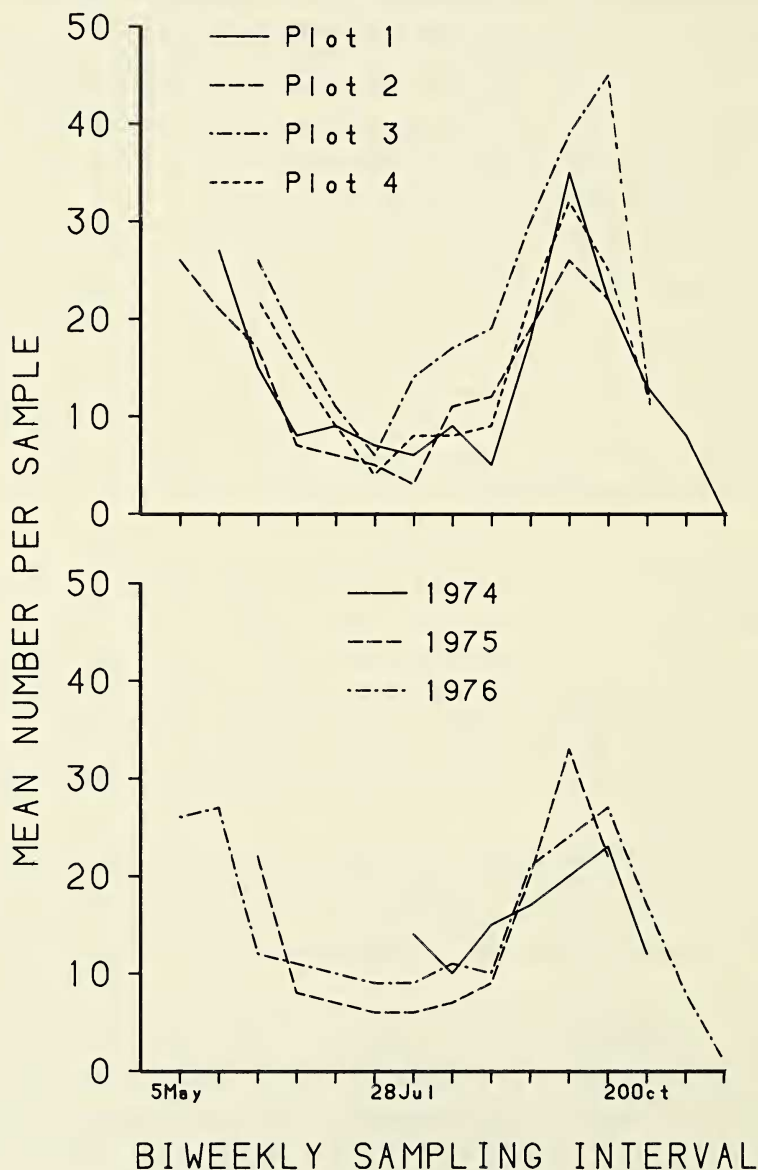


Fig. 6.—Seasonal abundance of herb stratum spiders in four study plots and three study years at Green Canyon, Cache Co., Utah.

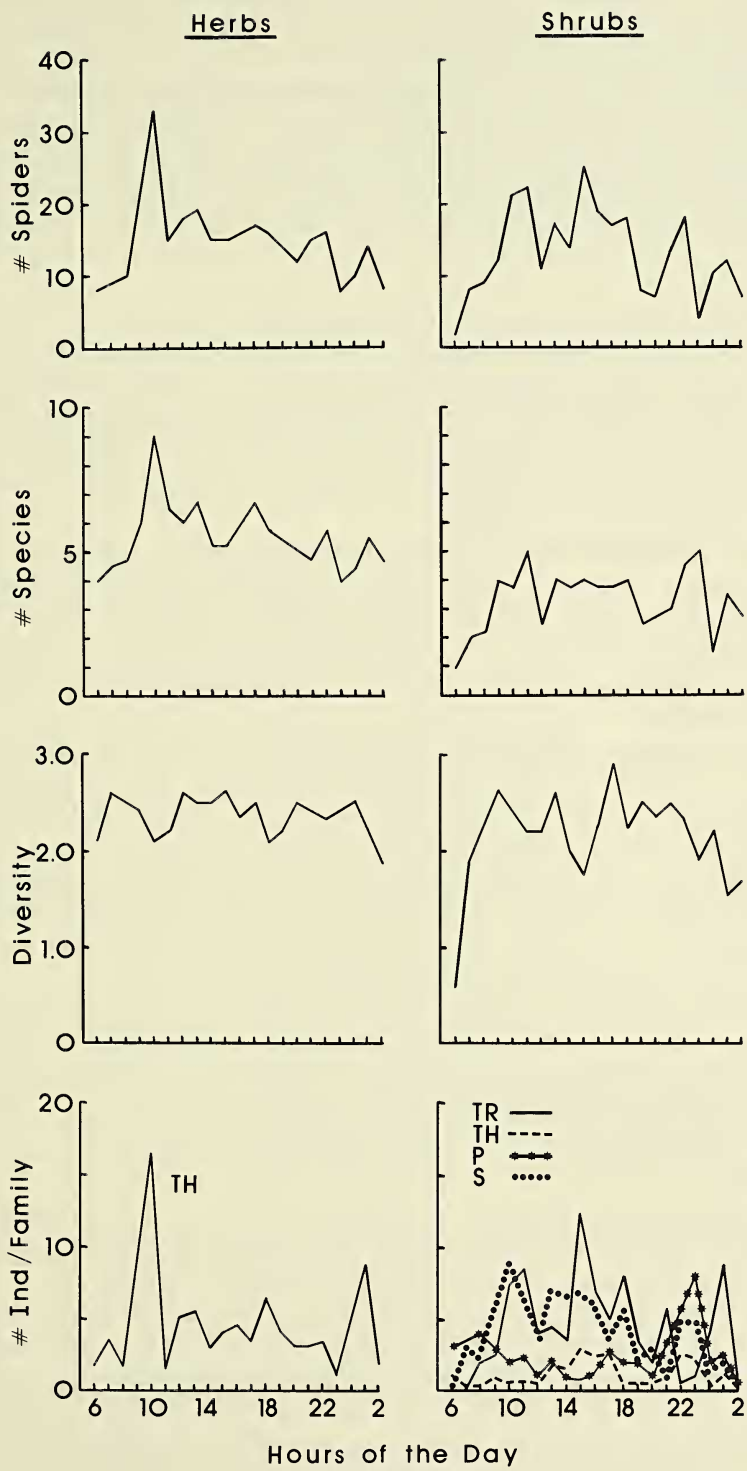


Fig. 7.—Abundance and diversity of herb and shrub stratum spiders through the day at Green Canyon, Cache Co., Utah. TH = Thomisidae; TR = Theridiidae; P = Philodromidae; S = Salticidae.

and increasing on the ground (Figure 5). The final decline in pitfall captures reflects winter inactivity. Captures of spiders on the ground began to decline when mean bi-weekly temperature fell below 5°C (Figure 2).

Species diversity of herb stratum spiders followed a pattern generally opposite to that of abundance, except for the winter decline (Figure 5). Hatley and MacMahon (1980) found a midseason peak in shrub spider diversity at Green Canyon. Although the seasonal diversity pattern shown by shrub spiders in the present study does not entirely match the above patterns, only a few shrubs were sampled during the apparent summer decline in diversity (Figure 5). If the data point for 30 June is low, these patterns would all match closely.

TIME OF DAY. Mean number of spiders per sample in herbs exhibited a significant peak at 1000 hr (Figure 7). Spider abundance was negatively correlated (linear regression) with hours of the day from 1000 to 0200 hr ($P = 0.01$, $r = -0.72$) and positively correlated from 0600 to 1000 hr ($P = 0.05$, $r = 0.90$). Although Thomisidae were collected most frequently at 1000 hr in herbs (Figure 7), this peak was not significant. Significant peak abundance of web spiders collected at this time probably made the total spider abundance curve significant at 1000 hr.

Correlations with microclimatic variables indicate that spider responses to light intensity, temperature and relative humidity interact to produce peak abundance in the herb stratum during late morning. At that time light intensity is high, but temperature is still lower and relative humidity higher than at similar light intensities in the afternoon. Light intensity was positively correlated to abundance of all important herb spider families except Philodromidae.

Abundance of spiders in shrubs was not correlated to time of day (Figure 7). This may have been due to the known moderating effect of shrubs upon microclimate allowing spiders to remain in the shrub stratum throughout the day. It may also have been due to the large number of web spiders in shrubs remaining in webs or retreats rather than migrating to another stratum to spend their inactive periods. A third possibility is dominance in shrubs being shared by families which were correlated positively (Theridiidae) and negatively (Philodromidae; $P = 0.001$) to light intensity. Philodromidae was collected significantly most often in shrubs at 2300 hr (Figure 7).

Lowrie (1971) cautioned that time of collection does not necessarily indicate time of spider activity. However, at least in the case of spiders with retreats, sampling would surely dislodge fewer inactive than active individuals (if activity affected sampling at all). The early morning dip in shrub spider diversity (Figure 7) may have resulted from collection of only species not in retreats. In herbs, spider species diversity did not vary as much through the day.

Conclusions: Temporal Patterns.—The phenology of herb stratum spiders of the sagebrush steppe seems to be adapted to avoid the hot, dry part of the year, with reproduction in the spring, the fall, or both. Some ground spiders, however, reproduce during the summer. Within each stratum, peak abundances of the several dominant families are offset (Figure 5). Ultimate factors such as competition between dominant families may play a part in this observed seasonal separation of reproductive periods.

Microclimate seems to be the most important proximate factor determining herb stratum spider abundance through the day. A more stable microclimate through the day, migration of spiders into shrubs, or competitive interactions, could result in the lack of correlation of shrub stratum spiders with time of day.

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Appendix.—Numbers and relative abundances (RA) of spider taxa collected from vertical strata of the sagebrush steppe at Green Canyon, Cache Co., Utah. Families are listed alphabetically under foraging strategies.

Spider Taxon	Herbs		STRATUM Shrubs		Ground	
	#	RA	#	RA	#	RA
Ambushers	2997	45.2	281	9.8	285	17.9
Antrodiaetidae	0	0.0	0	0.0	30	1.9
<i>Antrodiaetus montanus</i> (Chamberlin & Ivie)	0	0.0	0	0.0	30	1.9
Mimetidae	5	0.1	0	0.0	1	0.1
<i>Mimetes atkinus</i> Chamberlin & Ivie	5	0.1	0	0.0	1	0.1
Thomisidae	2992	45.1	281	9.8	254	16.0
<i>Misumenops asperatus</i> (Hentz)	41	0.6	3	0.1	0	0.0
<i>M. lepidus</i> (Thorell)	2062	31.1	158	5.5	5	0.3
<i>Xysticus cunctator</i> Thorell	872	13.2	118	4.1	62	3.9
<i>X. gulosus</i> Keyserling	16	0.2	0	0.0	13	0.8
<i>X. montanensis</i> Keyserling	1	0.0	2	0.1	174	10.9
Wanderers	1665	25.1	1638	57.0	1102	69.3
Anyphaenidae	51	0.8	33	1.2	5	0.3
<i>Anyphaena pacifica</i> Banks ¹	51	0.8	33	1.2	5	0.3
Clubionidae	46	0.7	47	1.6	93	5.8
<i>Castianeira occidens</i> Reiskind	0	0.0	0	0.0	57	3.6
<i>Chiracanthium inclusum</i> (Hentz)	46	0.7	47	1.6	2	0.1
<i>Phrurotimpus alarius</i> (Hentz)	0	0.0	0	0.0	33	2.1
Unidentified	0	0.0	0	0.0	1	0.1
Gnaphosidae	7	0.1	15	0.5	409	25.7
<i>Drassodes saccatus</i> (Emerton)	1	0.0	0	0.0	9	0.6
<i>Drassyllus insularis</i> (Banks)	0	0.0	0	0.0	51	3.2
<i>D. nannellus</i> Chamberlin & Gertsch	0	0.0	1	0.0	165	10.4
<i>Gnaphosa sericata</i> (L. Koch)	0	0.0	0	0.0	30	1.9
<i>Haplodrassus signifer</i> (C. L. Koch)	3	0.0	0	0.0	105	6.6
<i>Herpyllus</i> sp.	1	0.0	6	0.2	0	0.0
<i>Micaria</i> sp. nov.	2	0.0	7	0.2	17	1.1
<i>Nodocion rufithoracica</i> (Worley)	0	0.0	0	0.0	3	0.2
<i>Poecilochroa montana</i> Emerton	0	0.0	0	0.0	1	0.1
<i>Zelotes subterraneus</i> (C. L. Koch)	0	0.0	1	0.0	27	1.7
Unidentified	0	0.0	0	0.0	1	0.1
Lycosidae	6	0.1	1	0.0	545	34.3
<i>Alopecosa kochi</i> (Keyserling)	0	0.0	0	0.0	13	0.8
<i>Lycosa</i> sp. ¹	0	0.0	0	0.0	1	0.1
<i>Pardosa wyuta</i> Gertsch	0	0.0	1	0.0	5	0.3
<i>Schizocosa wasatchensis</i> Chamberlin & Ivie	6	0.1	0	0.0	526	33.1
Oxyopidae	50	0.8	120	4.2	1	0.1
<i>Oxyopes scalaris</i> (Hentz)	50	0.8	120	4.2	1	0.1
Philodromidae	845	12.7	508	17.7	23	1.4
<i>Ebo evansae</i> Saur & Platnick	0	0.0	3	0.1	0	0.0
<i>E.</i> sp.	5	0.1	35	1.2	0	0.0
<i>Philodromus californicus</i> Keyserling	9	0.1	1	0.0	1	0.1
<i>P. histrio</i> (Latreille)	435	6.6	307	10.7	5	0.3
<i>P. satullus</i> Keyserling	4	0.1	20	0.7	0	0.0
<i>P. speciosus</i> Gertsch ¹	1	0.0	18	0.6	0	0.0
<i>P. rufus</i> Walckenaer	3	0.1	3	0.1	0	0.0
<i>Thanatus formicinus</i> (Clerck)	33	0.5	28	1.0	15	0.9
<i>Tibellus chamberlini</i> Gertsch	135	2.0	18	0.6	0	0.0
<i>T. oblongus</i> (Walckenaer)	220	3.3	75	2.6	2	0.1

Salticidae	660	10.0	914	31.8	26	1.6
<i>Icius similis</i> Banks	1	0.0	0	0.0	0	0.0
<i>Metaphidippus aeneolus</i> (Curtis)	122	1.8	144	5.0	0	0.0
<i>M. verecundus</i> (Chamberlin & Gertsch)	14	0.2	18	0.6	0	0.0
<i>M. sp.</i>	26	0.4	7	0.2	0	0.0
<i>Pellenes hirsutus</i> (Peckham & Peckham)	50	0.8	7	0.2	6	0.4
<i>Phidippus johnsoni</i> (Peckham & Peckham)	122	1.8	54	1.9	1	0.1
<i>P. octopunctatus</i> (Peckham & Peckham)	1	0.0	1	0.0	9	0.6
<i>Sassacus papenhoei</i> (Peckham & Peckham)	277	4.2	520	18.1	0	0.0
<i>Synagales sp. nov.</i>	44	0.7	157	5.5	0	0.0
<i>Talanera minuta</i> Banks	1	0.0	0	0.0	10	0.6
Unidentified	2	0.0	6	0.2	0	0.0
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Webspinners	1971	29.7	955	33.2	204	12.8
Agelenidae	0	0.0	0	0.0	46	2.9
<i>Cicurina intermedia</i> Chamberlin & Ivie	0	0.0	0	0.0	46	2.9
Amaurobiidae	0	0.0	0	0.0	4	0.2
<i>Titanoeca nigrella</i> (Chamberlin)	0	0.0	0	0.0	4	0.2
Araneidae	634	9.6	56	2.0	1	0.1
<i>Aculepeira verae</i> Chamberlin & Ivie	130	2.0	12	0.4	0	0.0
<i>Araneus gemma</i> (McCook)	15	0.2	2	0.1	0	0.0
<i>Araniella displicata</i> (Hentz)	29	0.4	1	0.0	0	0.0
<i>Argiope trifasciata</i> (Forsk.)	43	0.6	9	0.3	1	0.1
<i>Hyposinga singaeformis</i> (Schaeffer)	19	0.3	7	0.2	0	0.0
<i>Larinia borealis</i> Banks	8	0.1	0	0.0	0	0.0
<i>Metepeira foxi</i> Gertsch & Ivie	389	5.9	24	0.8	0	0.0
<i>Neoscona arabesca</i> Walckenaer	1	0.0	1	0.0	0	0.0
Dicynidae	356	5.4	35	1.2	0	0.0
<i>Dictyna completa</i> Chamberlin & Gertsch	173	2.6	22	0.8	0	0.0
<i>D. idahoana</i> Chamberlin & Ivie	182	2.7	11	0.4	0	0.0
Unidentified	0	0.0	1	0.0	0	0.0
Unidentified	1	0.0	1	0.0	0	0.0
Linyphiidae	388	5.8	68	2.4	87	5.5
<i>Erigone dentosa</i> O. Pickard-Cambridge	345	5.2	56	2.0	13	0.8
<i>Frontinella communis</i> (Hentz)	2	0.0	0	0.0	5	0.3
<i>Meioneta sp. 1</i>	16	0.2	6	0.2	18	1.1
<i>M. sp. 2</i>	0	0.0	1	0.0	1	0.1
<i>M. sp. 3</i>	1	0.0	1	0.0	3	0.2
<i>Spirembolus mundus</i> Chamberlin & Ivie	21	0.3	4	0.1	43	2.7
Unidentified	1	0.0	0	0.0	0	0.0
Unidentified	2	0.0	0	0.0	3	0.2
Unidentified	0	0.0	0	0.0	1	0.1
Pholcidae	0	0.0	0	0.0	13	0.8
<i>Psilochorus utahensis</i> Chamberlin	0	0.0	0	0.0	13	0.8
Tetragnathidae	19	0.3	3	0.1	0	0.0
<i>Tetragnatha laboriosa</i> (Hentz)	19	0.3	3	0.1	0	0.0
Theridiidae	574	8.6	793	27.6	53	3.3
<i>Dipoena tibalis</i> Banks ¹	11	0.2	22	0.8	0	0.0
<i>Enoplognatha ovata</i> (Clerck)	8	0.1	3	0.1	0	0.0
<i>Euryopsis scriptipes</i> Banks	9	0.1	4	0.1	0	0.0
<i>Latrodectus hesperus</i> Chamberlin & Ivie	49	0.7	1	0.0	43	2.7
<i>Steatoda americana</i> (Emerton)	30	0.4	3	0.1	6	0.4
<i>Theridion albidum</i> Banks	2	0.0	0	0.0	0	0.0
<i>T. neomexicanum</i> Banks	460	6.9	715	24.9	3	0.2
<i>T. petraeum</i> L. Koch + <i>T. rabuni</i> Chamberlin & Ivie ²	5	0.1	45	1.6	1	0.1

1) Probable identification (—W. J. Gertsch)

2) Author unable to separate species (majority immatures)